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HYBRIDISM AND THE RATE OF EVOLUTION IN ANGIOSPERMS

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IN responding to an invitation to contribute to the morning program of the American Society of Naturalists, it has seemed to me that a statement emphasizing some of the morphological features of the greatest of all biological problems, the *modus operandi* of the process of evolution, would be of interest to my fellow biologists. The most distinguished as well as the most profound investigator, which our science has yet produced, Charles Darwin, has unequivocally expressed the opinion in the "Origin of Species," that morphology is the soul of natural history. As I am addressing a body of men who call themselves naturalists, my theme will, I hope, not appear unimportant.

The rate of evolution has not been the same at all periods of our earth's history. There is an agreement among those whose knowledge of the vegetable population of earlier eras makes their opinion worthy of serious regard, that the plant kingdom in former times was in a much less rapid condition of evolutionary change than in the present age. Within the limits necessarily assigned to me it is impossible to state all the probable causes of this notable acceleration in the rate of change in plants. I shall touch only upon two aspects of this problem and of these I shall be able to develop but one.

Extremely important factors in the evolution of plants

have unquestionably been the progressive cooling of our earth's surface, as well as those recently recognized secular periodic twilights of the sun god, known as glacial periods. The latter have worked in an exterminating manner and have wiped out well nigh completely whole types of plants and have left the way clear for the unrestricted development of better adapted forms. For example, at the end of the Paleozoic, in the late Permian, we find world-wide evidence of glaciation, which resulted in the virtual extinction of the great cryptogamic forests, which contributed the raw materials of our most abundant coals. With the passing of the arboreal Cryptogams, the Gymnosperms became the predominant element of the world forests in the Mesozoic. At the end of the Cretaceous there was another age of extinction, which wiped out the mass of Gymnosperms and particularly the Conifers. The naked seeded plants, which prevailed in the medieval period of our earth's history, have in the vegetation of to-day been reduced in the number of species to the merest fraction of seed-producing plants; which in the present age are overwhelmingly angiospermous.

From the present standpoint, however, the progressive but not spasmodic cooling of our earth is of even greater importance. Investigations initiated in my laboratories have made it clear that herbaceous Angiosperms have been derived from woody ones as a response to the increasing coldness of terrestrial climates. Plants of this organization are of such efficiency that they are able to go from seed to seed in a few weeks and thus pass through the inclement winter season in a resting stage. The original researches in this direction were undertaken by Professor Eames. The theme in the past two years has undergone a profitable exploitation by other former students in both botanical and geological publications. The origin of the herbaceous type in the Angiosperms has in itself added a notable impetus to the rate of evolution in the group. Whatever hypothesis one adopts as to the mode of the origin of species, it is quite clear that the

multiplication of generations as well as of individuals, rendered possible by the appearance of the herbaceous type of small size and short reproductive cycle, will contribute to the acceleration of evolutionary processes.

A noteworthy feature, which distinguishes the huge aggregation of Angiosperms now inhabiting the surface of the globe (in the neighborhood of one hundred and forty thousand species) from the saved remnant of the Gymnosperms, is their inherent variability. This high degree of variability has naturally made the Angiosperms a very difficult group from the systematic standpoint and has likewise put them in the foreground in connection with discussions as to the origin of species. Two of the oldest tribes of the coniferous Gymnosperms are the pines and the araucarians. I have had the good fortune to be able to make a careful comparison of structure extending to all important details, between living representatives of these tribes and their predecessors in the Cretaceous of the eastern United States. It is quite clear from these studies that the genus *Pinus* and the genus *Araucaria* in the remote times of the Age of Chalk, differed only in the smallest particulars from their living descendants. The conclusion inevitably follows that the course of evolution here has been very slow. The actual situation corresponds accurately with the data derived from the past. A white pine, compared with an evening primrose or a rose, is relatively constant and invariable.

The remarkable variability of the Angiosperms, as frequently expressed in terms of the difficulty of systematic identification, brings us naturally to the much debated question of the origin of variability. Darwin, as is well known, simply accepted this phenomenon as a fact and did not, after the first, at any rate, attempt to explain the condition in terms of other phenomena. It is interesting, however, to note that in the beginning he was disposed to accept hybridization as the cause of the variability of species and apparently abandoned this belief only because he could find no evidence for its occurrence on a suffi-

ciently extensive scale. Quite recently the view that heterozygosis is responsible for the mutability of species has again been advanced by Lotsy in an interesting article published in the *Archives Néerlandaises*. This author very definitely takes the position that variability in general is due to hybridization, and that true species (not necessarily those of Linnæus and other systematists) are invariable. With this view I am personally in agreement, with the limitation that the statement goes much too far.

It is one of the commonplaces of breeding that the offspring resulting from hybridization is extremely variable and may be characterized by a greater or less degree of sterility. Taking the particular case of the Angiosperms, it is found that when species of lilies, irises, honeysuckles, etc., are crossed, the result is a highly mutable progeny with a greater or less degree of sexual sterility, the latter condition most easily recognized in the microspores or pollen. The main purpose of the present statement is to make it clear to my fellow naturalists that in nature a high degree of variability often exists in the case of the Angiosperms, expressed either in terms of difficulty of systematic determination in view of intergrading forms, or often in the less obtrusive form of multiplication of species in a given genus. This extreme degree of variability is very largely accompanied by the highly significant phenomenon of pollen sterility.

A family of Angiosperms much in the foreground in recent years is the Onagraceæ or Evening Primrose family. In the case of the genus *Oenothera* remarkable conditions have been discovered by De Vries. The plants of *O. lamarckiana*, when grown in large numbers, show a number of individuals, sometimes as high as one twentieth of the total number, markedly different in character from typical *O. lamarckiana*. This phenomenon was at first thought to be peculiar to this species of *Oenothera* and a great deal of importance was consequently attached to clearing up its somewhat dubious systematic position.

Fortunately we are relieved from the uncertainties necessarily connected with this kind of investigation, by the discovery in more recent years that other and perhaps all species of the genus possess the same features. The activity of systematic botanists in recent years in making new species of *Ænothera* is highly significant in the present connection. The exceptional individuals which grow up in cultures of species of *Ænothera* have been termed by De Vries and his disciples "elementary species." The biological world has been asked to believe that in the appearance of these new forms in cultures of *Ænothera*, we have the phenomenon of mutation or the origin of species at a leap. This view of the matter is, however, open to serious question. The species of *Ænothera*, as well as their so-called mutants, are distinguished by a degree of pollen sterility often extreme. This condition has convinced so accomplished a geneticist as Professor Bateson that the so-called elementary species of *Ænothera* are segregates resulting from previous hybridization. This view of the matter is supported by the fact that the products of hybridization are often relatively fixed forms, as indeed has been noted by Brainerd in his extremely interesting observations on hybrid wild violets.

Obviously the question of possible mutation in the genus *Ænothera* entered into a new and biologically more advantageous phase when other species than *O. lamarckiana* came into the discussion. Clearly a still wider view should even more clarify the situation. Two years ago Miss Ruth Holden, who is at present living in Cambridge, England, made the interesting discovery that the common fireweed, *Epilobium angustifolium*, growing wild near Cambridge and also cultivated in the Cambridge botanic garden, was characterized by a large degree of sterility of pollen. She at once generously communicated her discovery to me and at the same time suggested a reason for the condition of pollen found in the English specimens of *Epilobium angustifolium*. I must here remind you that under the genus *Epilobium* are included two distinct

subgenera, namely *Chamænerion*, distinguished, among other features, by its distinct pollen grains; and *Epilobium* proper having its pollen grains in groups of four. *E. angustifolium* belongs to the section *Chamænerion*, and in the southern part of Canada and the Northern States has no allied species except in mountainous regions (*e. g.*, mountainous Quebec and Colorado). Acting on the suggestion supplied by Miss Holden's discovery, Mr. C. A.

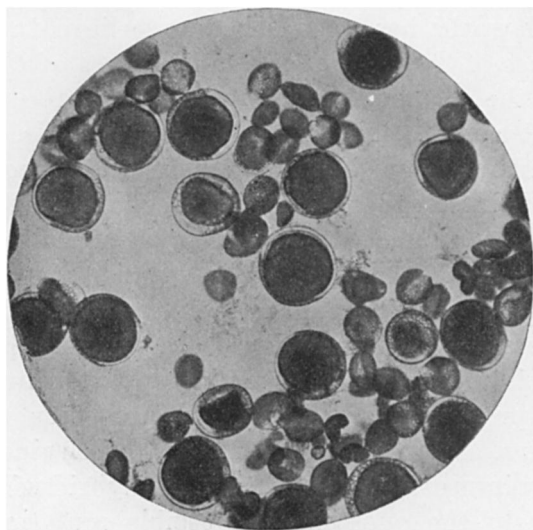


FIG. 1. Pollen of hybrid *Iris germanica*.

Forsaitb, one of my graduate students, has investigated the conditions of sterility found in species of *Epilobium* belonging to the section of *Chamænerion*. Through the kindness of the Gray Herbarium of Harvard University he has been able to study some two hundred specimens from various geographic regions. The conditions in *Epilobium* (*Chamænerion*) *angustifolium* in the northern part of its range, where it coincides in distribution with its allied species, *E. latifolium*, are most interesting. Nearly nine tenths of the specimens showed the pollen to be imperfect. In contrast, the material from the southern limits, where *E. angustifolium* does not coincide in distri-

bution with *E. latifolium*, are almost uniformly characterized by a high degree of perfection. To be specific, specimens from Ontario, western Quebec, and New Hampshire and Massachusetts show pollen perfectly developed or at most with a few grains disorganized. Mr. Forsaith extended his investigation, again through the courtesy of the Gray Herbarium, to the other genera and species of the Onagraceæ, with similar results. The investigation as a whole will be described elsewhere, but it will be necessary



FIG. 2. Pollen of *Zauschneria californica*, a monotypic representative of the Onagraceæ.

to consider a few more illustrations in the present connection. There is one quite monotypic species in the order, namely *Zauschneria*. It was found that in this the pollen is practically perfect and the same state of affairs is present in the two geographically limited species of *Gongylocarpus*, one occurring in Vera Cruz and the other on the opposite side of the continent in Lower California. The general situation in the case of the Onagraceæ, a family much in the foreground at the present time by reason of the investigations of De Vries and his disciples, is that monotypic species or those geographically isolated have

perfect pollen and are little characterized by variability; while where the species are numerous and coincident in their range both variability and pollen sterility are conspicuous.

We may now consider another highly variable group, which has not infrequently been called a hybrid family, namely the Rosaceæ. The genera *Rosa*, *Rubus* and *Crataegus* are notable for the extreme difficulty they have offered from the systematic point of view. Three of my

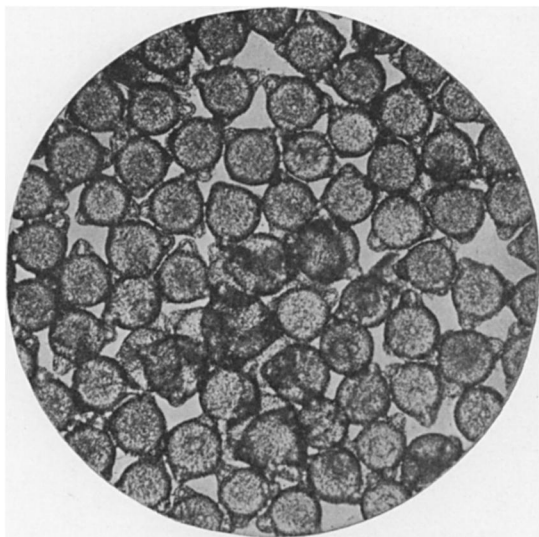


FIG. 3. Pollen of *Chamaenerion* (*Epilobium*) *angustifolium* from Massachusetts.

graduate students have investigated these genera and the

results may be conveniently summarized by reference to the genus *Rubus*. In the case of *Rubus*, in regions where it has been exhaustively studied, there is almost no end to the species which may be set up. In Europe, in fact, the species have mounted into the thousands. The situation may for the sake of brevity be considered under three heads. First, there are species which range together and have flowering periods which overlap—a condition common to the mass of our ordinary *Rubi*. In *Rubus villosus*,

the blackbriar, and *R. strigosus*, the wild red raspberry, both very variable species, the pollen is extremely bad. Where these species occur on islands, however, the pollen is generally much more perfect, probably as the result of isolation. I have noticed, for example, that *R. villosus* and *R. strigosus* from Cape Breton Island have considerably better pollen than that found in the case of continental material of the same two species. What is true of these particular species holds more or less well for a

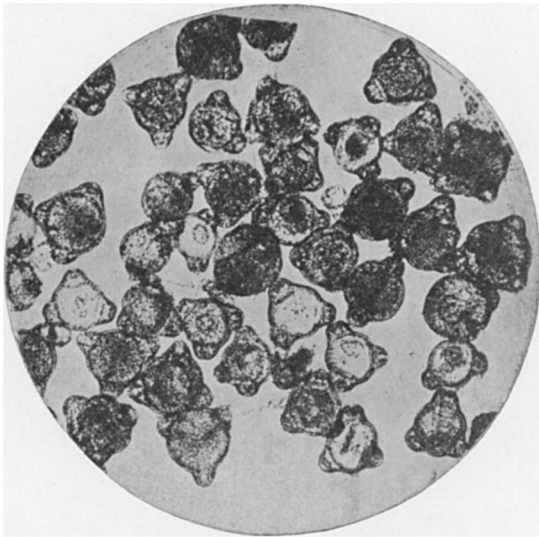


FIG. 4. Pollen from *Chamaenerion (Epilobium) angustifolium* from the vicinity of Cambridge, England, showing abortive grains.

large number of others of similar range and flowering periods. Next may be considered a species of limited geographic range, namely *R. deliciosus* from the Rocky Mountains. Here the pollen is practically entirely perfect, a few defective elements being occasionally found. Last may be described *R. odoratus*, the so-called flowering raspberry, which blossoms after the mass of other species have shed their flowers. Here, as one might expect, the pollen is highly perfect and practically unmingled with shrivelled grains. A general study of the Rosacæ, which can not even be summarized in the brief

time at my disposal, shows clearly that propinquity, geographical or phenological, is to a large extent correlated with pollen imperfection in the group.

Limitations of time make it necessary to proceed summarily with other illustrations. Next may be cited the Betulaceæ and Fagaceæ. Each of these orders has one strikingly polytypic species, *Betula* in the one case, and *Quercus* in the other. Interestingly enough, it is in these two genera that variability and gametic sterility coincide.

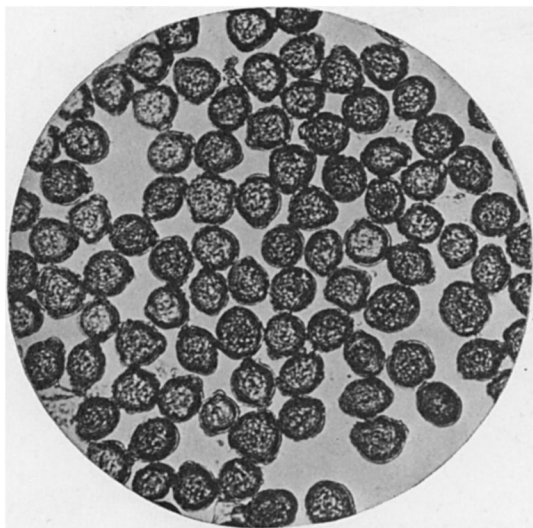


FIG. 5. Pollen of *Rubus deliciosus* from the Rocky Mountains, showing well developed grains.

One might continue at length through the Dicotyledons, but one other example must suffice for this division of the Angiosperms. The Solanaceæ have one huge genus, *Solanum* itself, in which there are nine hundred species. In this genus not only is there extreme variability, but also a large degree of pollen sterility. In the monocotyledonous division we may start with the grasses. Monotypic grasses have perfect pollen, as is illustrated, for example, by the wild rice, *Zizania aquatica*. In the genus *Alopecurus*, with numerous and propinquitous species, on the contrary the pollen conditions frequently indicate gen-

etical contamination. Proceeding to aquatics, in the Potamogetonaceæ, the monotypic *Zannichellia* and *Zostera* have perfectly developed microspores; while *Potamogeton*, with its numerous species, is often distinguished by a large degree of pollen imperfection. Similar statements hold in a like sense in regard to members of the Alismaceæ, Sparganiaceæ, etc.

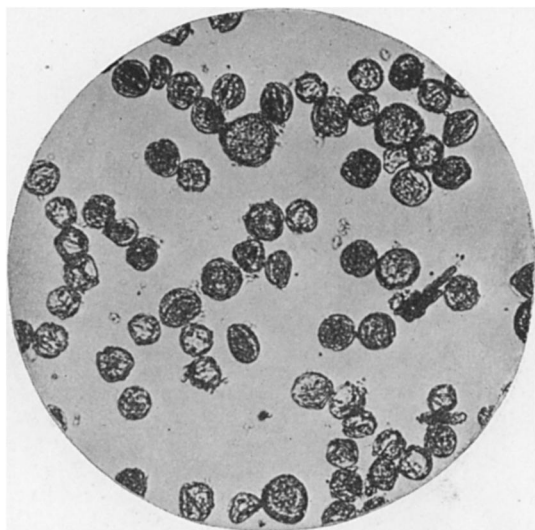


FIG. 6. Pollen of *Rubus villosus* (Blackbriar), showing high degree of imperfection.

The pressure of time compels a summing up of the situation without further references to detailed facts, which will be supplied by publications soon to appear. The general condition in the Angiosperms in contrast to the Gymnosperms is a large degree of variability in the species. Where the species are highly inconstant and cause great difficulty to the systematist, as, for example, in the Onagraceæ, Rosaceæ, Solanaceæ, Birches, Oaks, etc., there is often a large degree of pollen sterility. Where isolation, geographical, phenological or specific, is present the contents of the anther sacs are strikingly perfect in their development. In other words, where interspecific crossing is possible, there is often clear evidence of its presence

in the form of a high degree of variability, accompanying a considerable manifestation of sterility in the gametic cells, particularly the pollen. In the numerous species of *Rosa* or *Oenothera*, we find in regard to both variability and the phenomenon of sterility, a marked contrast to the also numerous species of the very old genus *Pinus*. In *Pinus* there is practically no imperfection in the develop-

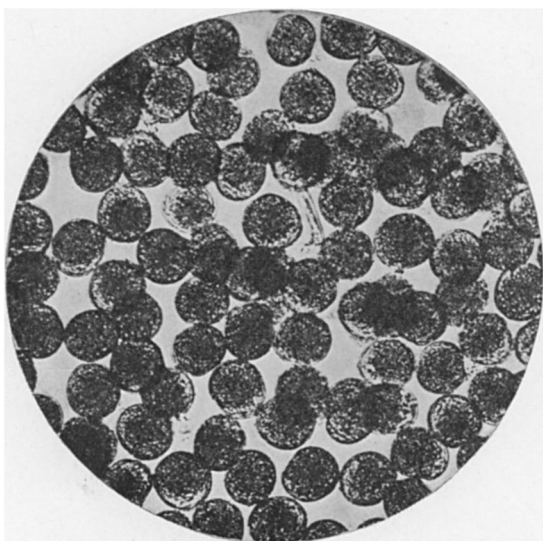


FIG. 7. Pollen of *Zizania aquatica*, a genus with few isolated species.

ment of the microspores, even in exotic species, and the species are very clearly marked and constant.

If associated variability and gametic sterility are reliable indications of hybridization, then it becomes clear that the Angiosperms, unlike the Gymnosperms and the mass of the vascular Cryptogams, are often characterized by heterozygosis. It has been recently suggested that pollen imperfection is not so much an evidence of hybridization as of mutability. This criticism appears to fail for various reasons. First, for nearly a hundred years practically all students of hybridization in plants have noted pollen sterility and imperfect development of the seed as peculiar characteristics of hybrids. Secondly,

in genera with often highly sterile species, such as *Rubus*, the species which are isolated for any reason from the rest have either perfect pollen or manifest a much less marked degree of sterility. An objection urged by De Vries to gametic degeneracy as a criterion of hybridism needs apparently only to be stated to supply its own refutation. The distinguished plant physiologist of Amsterdam, in a recent article in which he criticizes the writer's

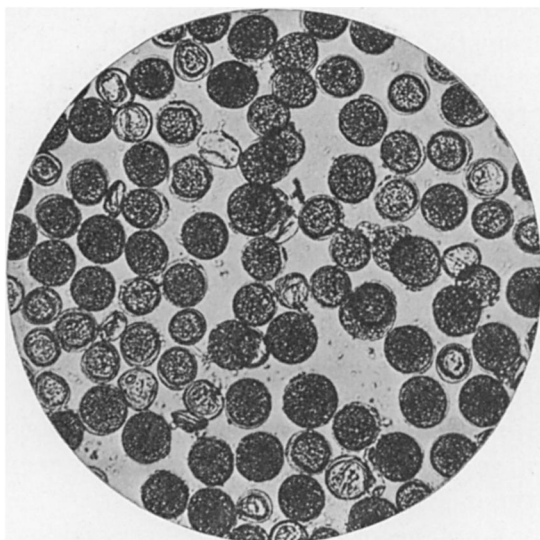


FIG. 8. Pollen of *Alopecurus pratensis*, showing high degree of imperfection which may occur in a polytypic genus.

attitude in regard to the intimate relation between defective pollen, hybridization and so-called mutation, somewhat superciliously, states that the degeneracy of spores in connection with the development of the megaspores of the heterosporous vascular Cryptogams (and one might add the seed plants as well) might with equal validity be regarded as evidence of hybridism in the megasporic sporangia. One has only to carry De Vries's argument to its logical conclusion to prove its entire fallacy. Since microsporic sporangia (in which there is no spore degeneration apart from hybridism) and megasporic sporangia occur ordinarily or at least primitively on the same plant,

it follows that so far as the phenomenon of spore degeneration is concerned some sporangia (the megasporangia or seeds) are of hybrid origin and others (the microsporangia or anthers) are not. The logical absurdity of this conclusion will be clear to every one.

There seems to be no question on the basis of the well-established criteria of hybridism, that many Angiosperms present clear indications that their species are of heterozygous origin. Since one of the most efficient methods of inducing variability in connection with the development of improved varieties of plants is hybridization, often on a very large scale, it seems not unreasonable to regard spontaneous hybridization in the Angiosperms (the evidences for which are so numerous and so impressive) as having an incalculably large effect on their rate of evolution. There is, however, apparently no reason for assuming a similar condition in the Gymnosperms and the vascular Cryptogams. The great and indeed overwhelming advantage which the Angiosperms have secured in the struggle for existence over the lower groups of vascular plants is apparently connected in an intimate way with hybridism on the one hand and the development of herbaceous types (in response to progressive climatic refrigeration) on the other. If this conclusion is correct we must reject the assumption of universal hybridism as the sole cause of variation put forward by Lotsy as much too sweeping. Small variations unquestionably characterize the Gymnosperms, and in the course of long geological time have availed in the absence of competition from heterozygous types, with a much greater range of variability and consequently a higher potentiality of evolution. It is obviously impossible for the homozygous Conifers to make headway against the characteristically heterozygous Angiosperms. The small variations of homozygous stocks clearly prevailed in the earlier history of our earth, while the more rapid changes which have ensued in later times are correlated, so far as plants are concerned, at any rate, with marked physiographic and

climatic differentiation, and most important of all with the phenomenon of heterozygosis.

In conclusion the situation may be summarized. The phenomenon of variation in the older types of plants is still unexplained and must apparently be accepted as an ultimate characteristic of living matter. In the case of those groups of plants, which have achieved predominance under the present climatic conditions of our earth, hybridism has clearly played a large rôle in the acceleration of the processes of evolution. The peculiar conditions presented by the species of *Ænothera*, which have been put forward by De Vries in favor of his mutation hypothesis, are obviously only a particular case of the manifestation of the natural hybridism, which is so widespread a feature of the Angiosperms. The mutation hypothesis has suffered a process of rapid disintegration of late and it is increasingly clear on the botanical side that where the term mutation is used it ordinarily indicates changes which are the result of previous hybridization. Concerning the Animal Kingdom the trend of opinion is apparently setting equally strongly against mutation. My zoological colleague, Professor Castle, has recently declared himself in no uncertain terms against the hypothesis of mutation, an expression of opinion not the less convincing because he originally held the view that mutation was a necessary pendant to Mendelism. He is now able to explain to himself the appearance of new characters as a result of the summation of small variations, which is essentially the Darwinian position.